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Für meine Eltern und meinen Bruder

Vigilance and feeding behaviour of Ruffs *Philomachus pugnax* during spring migration in Eastern Austria

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Abstract This study tested for effects of flock size and other potentially important variables (location, vegetation cover, wind force, cloud cover, date, time and feeding habitat) on vigilance level and food intake of foraging Ruffs *Philomachus pugnax* during spring migration at Seewinkel, an important stopover site for waders in Eastern Austria. Therefore, foraging Ruffs were filmed at four different salt ponds. Finally, a total of 681 film sequences were available for analysis. The two main components of foraging behaviour, vigilance and food intake, measured as scan rate (number of scans per 30 sec) and peck rate (number of pecks per 30 sec), respectively, were not correlated. To test for effects of predictor variables on scan and peck rate of foraging Ruffs Generalized Linear Models (GLMs) were calculated including all variables and all possible subsets. Three variables remained in the 12 best GLMs (selected according to Akaike´s Information Criterion) testing for effects on scan rate of foraging Ruffs: feeding location, feeding habitat and flock size. These variables also significantly affected Ruffs´ scan rates according to Wald statistics. Besides differences of scan rates between feeding locations, vigilance level was significantly higher in terrestrially foraging Ruffs than in birds feeding at semi-aquatic habitat patches. Furthermore, scan rate decreased with increasing flock size. To test for effects of the eight aforementioned predictor variables on peck rate, the mobility of Ruffs during foraging quantified as number of steps per 30 sec was included in all calculated GLMs. Four of the nine predictor variables remained in the best model: location, wind force, cloud cover and date. Two of them, feeding location and wind force, were included in all 23 best models and had a strong effect on peck rate according to Wald statistics. Peck rate increased with increasing wind force. GLMs to assess effects of moult stage and colour morph of males (indicating their social status) on vigilance and peck rate additionally only included predictor variables,

which already proved to have a significant effect on scan and/or peck rate (location, feeding habitat, flock size, cloud cover and wind force). Furthermore, we included the date as predictor variable and allowed for a two-way interaction between date and moult stage and male plumage colour, respectively, because both the proportion of birds with different moult stage and birds belonging to different colour morphs changed with progressing spring migration. Calculated GLMs did not indicate any significant effects of moult stage or social status of males on scan and peck rate. Our study emphasized that even when controlled for other variables affecting scan rates, flock size still remains important for explaining variance in vigilance levels of foraging Ruffs. In contradiction, flocking did not directly affect food intake rate. However, stepping rate of birds decreased with increasing flock size indicating a better access to prey at sites where larger flocks aggregate. This is confirmed by the observation that food intake indeed increased with declining stepping rate. Furthermore, our observation that Ruffs´ vigilance and food intake significantly differed between salt pans has important implications for conservation.

Keywords Feeding habitat, flocking, food intake, foraging behaviour, moult, peck rate, scan rate, Seewinkel, social status, soda ponds, stepping rate, wind force

Zusammenfassung Die vorliegende Studie testete Effekte von Truppgröße und anderen potentiell wichtigen Variablen (Standort, Vegetationsbedeckung, Windstärke, Bewölkung, Datum, Tageszeit und Nahrungshabitat) auf das Sicherungsverhalten und die Nahrungsaufnahme von Kampfläufern *Philomachus pugnax* während des Frühjahrszuges im Seewinkel, einem wichtigen Rastplatz für Limikolen in Ostösterreich. Hierfür wurden Kampfläufer während der Nahrungssuche an vier Salzlacken gefilmt. Insgesamt standen 681 Filmsequenzen für Analysen zur Verfügung. Die zwei Hauptkomponenten des Furagierverhaltens, Sichern und Nahrungsaufnahme, quantifiziert als Sicherungsrate (Häufigkeit von Sicherungsverhalten pro 30 s) bzw. Pickrate (Häufigkeit von Pickverhalten pro 30 s), waren nicht korreliert. Um Effekte der Prädiktorvariablen auf Sicherungs- und Pickrate furagierender Kampfläufer zu testen, wurden Generalisierte Lineare Modelle (GLMs) berechnet, wobei alle Variablen und alle möglichen Kombinationen von Teilmengen der berücksichtigten Variablen inkludiert wurden. Drei Variablen verblieben in den 12 besten GLMs (ausgewählt nach dem Akaike

Informationskriterium) zum Testen von Effekten auf die Sicherungsrate von Kampfläufern: Standort, Nahrungshabitat und Truppgröße. Diese Variablen hatten nach der Wald-Statistik auch einen signifikanten Effekt auf die Sicherungsrate. Neben Unterschieden der Sicherungsrate zwischen den Standorten, wiesen am Land furagierende Kampfläufer eine signifikant höhere Sicherungsrate auf als semi-aquatisch furagierende Vögel. Zudem nahm die Sicherungsrate mit zunehmender Truppgröße ab. Um Effekte der vorher erwähnten Prädiktorvariablen auf die Pickrate zu testen, wurde die Mobilität der Kampfläufer während der Nahrungssuche – quantifiziert als Anzahl an Schritten pro 30 s – in die Modellselektion miteinbezogen. Vier der neun Prädiktorvariablen blieben im besten Modell: Standort, Windstärke, Bewölkung und Datum. Zwei von ihnen, Standort und Windstärke, waren in allen 23 besten Modellen inkludiert und hatten nach der Wald-Statistik einen starken Effekt auf die Pickrate. Die Pickrate stieg mit zunehmender Windstärke an. Um zusätzlich mögliche Effekte von Mauserstatus bzw. Gefiederfärbung der Männchen (als Indikator für ihren sozialen Status) auf Sicherungs- und Nahrungsaufnahmerate zu evaluieren, wurden nur jene Präditorvariablen herangezogen, die bereits einen signifikanten Effekt auf die Sicherungs- und/oder Pickrate zeigten (Standort, Nahrungshabitat, Truppgröße, Bewölkung und Windstärke). Außerdem wurde das Datum als Prädiktorvariable miteinbezogen und eine gegenseitige Interaktion zwischen Datum und Mauserstatus bzw. männlicher Gefiederfärbung zugelassen, da sich der Anteil an Vögeln in den verschiedenen Mauserstadien und Farbmorphen mit fortschreitendem Frühjahrszug änderte. Berechnete GLMs zeigten keine signifikanten Effekte des Mauserstatus oder des sozialen Status der Männchen auf die Sicherungs- und Pickrate. Unsere Arbeit hebt - bei gleichzeitiger Berücksichtigung anderer Variablen, die die Sicherungsrate beeinflussen - die Bedeutung der Truppgröße hervor, um die Varianz der Sicherungsrate von furagierenden Kampfläufern zu erklären. Im Gegensatz dazu hatte die Truppgröße keinen direkten Effekt auf die Nahrungsaufnahmerate. Jedoch nahm die Schrittzahl der Vögel mit zunehmender Truppgröße ab, was als Hinweis auf bessere Nahrungsverfügbarkeit an jenen Standorten, an denen sich größere Trupps bilden, gewertet werden kann. Das wird auch durch die Beobachtung verstärkt, dass die Nahrungsaufnahmerate mit abnehmender Schrittzahl anstieg. Außerdem ist unsere Beobachtung, dass sich das Sicherungs- und Nahrungsaufnahmeverhalten von

Kampfläufern zwischen den Salzlacken signifikant unterschied, von wichtiger Bedeutung für etwaige Schutzmaßnahmen.

Introduction

Like many other shorebirds Ruffs *Philomachus pugnax* are long-distance migrants (van Gils and Wiersma 1996). They cover up to 11,000 km on migration routes between their wintering areas in Southern Africa and their breeding grounds in Northern Europe and Siberia (Scheufler and Stiefel 1985). In the course of migration long-distance flights are interrupted by filling up fat reserves at suitable stopover sites before continuing migration (Weber et al. 1998). At stopover sites migrants have to cope with varying prey availability, inter- and intraspecific competition for limited resources and predation pressure (Lyons and Haig 1995). Furthermore, migratory birds are under time pressure on spring migration (e.g. Muraoka et al. 2009). With increasing latitude the time window of high prey availability, and consequently the time period suitable for breeding, is shortening (Newton 2008). Therefore, birds breeding at higher latitudes have to finish the entire reproduction cycle including the successful occupation of territories, mate acquisition and rearing of offspring at a shortened period of time. Hence, birds may try reaching their breeding grounds as early as possible to take advantage of the time favourable for breeding. In consequence, the time schedule for spring migration is strongly constrained by selective pressures related to the approaching reproductive period (Lyon and Haig 1995; Muraoka et al. 2009).

Since about 90 % of total migration time is spent on feeding and resting (Hedenström and Alerstam 1997), migration speed is mainly determined by fuel deposition rates at stopover sites in order to gain an adequate level of energy to carry the individual to the next stopover site or to the end of the migration journey (Lyon and Haig 1995). Therefore, migratory birds try to achieve high fuel deposition rates through increasing food intake rate, total daily feeding time, or both (Kvist and Lindström 2000). At stopover sites, birds face a potential trade-off between vigilance and feeding behaviour. Birds increasing their food intake rate may spend less time on other activities such as vigilance (Roberts 1996). However, high vigilance may be particularly important at stopover sites visited by larger numbers of migrating birds. Here, enhanced predation can be an important mortality factor in migrating birds (Alerstam et al. 2003). The main predators on small shorebirds during passage are raptors, especially medium-sized falcons and accipitors (Cresswell and Whitfield 1994). Raptors often attack waders when they are feeding at a short distance from

coverage. That increases the probability for raptors of not being detected by foraging waders within the time they need to attack (Whitfield 2003). In response, waders should select open areas away from cover as feeding sites to decrease predation risk, even though they may be poor in food supply (Whitfield 2003), or should increase vigilance when foraging closer to cover.

Another behavioural adaptation of foraging birds to decrease predation risk is flocking (Caraco et al. 1980a). Flocking enhances the chance of an earlier detection of a predator because more eyes are available for scanning the surrounding ("many eyes hypothesis"; Pulliam 1973). Furthermore, birds in flocks may profit from the dilution effect (Hamilton 1971) that keeps the risk for a particular bird being chosen by a predator lower in a large group than in a smaller one. As consequence, birds in larger flocks adapt their vigilance by decreasing scan rate (e.g. Randler 2005; Dias 2006; Sansom et al. 2008; but see Robinette and Ha 2001) and, therefore, have more time for other activities like feeding (Pulliam 1973).

How effectively waders adapt their foraging behaviour to the complex interactions of biotic and abiotic factors characteristic for individual stopover sites, determines the success of migration, which is ultimately measured in units of time and condition during passage and upon arrival at the destination (Smith and Moore 2003). This study aimed to analyse if, how and to which extent the variables flock size, feeding location, weather conditions, vegetation cover, date, time and habitat patch selection affect foraging behaviour of Ruffs *Philomachus pugnax* during spring migration at Seewinkel, an important stop-over site for waders in Eastern Austria (Laber 2003). In contradiction to other studies, which focused mainly on effects of single or a small number of biotic and/or abiotic variables on the foraging behaviour of birds (e.g. Beauchamp 1998; Evans 1976; but: Ward and Low 1997), our study evaluated effects of a large set of different factors potentially influencing vigilance and food intake of foraging Ruffs.

Food intake as quantified by birds´ peck rates can be affected by intraspecific competition. In foraging Redshanks *Tringa totanus* an increase of flock size can cause a decline of prey accessibility. Birds compensate for this by a higher mobility, measured as stepping rate, to reach habitat patches with better access to prey (Minderman et al. 2006). Therefore, stepping rate was suggested to be a good indicator of competition in foraging Redshanks. In this study we tested if stepping rate is increasing with flock size, which could indicate a potential decrease of food

availability when a habitat patch is (over-)exploited by a larger flock. Then stepping rate might be also negatively related to food intake quantified as peck rate.

Additionally, possible effects of moult stage and social status of Ruffs on foraging behaviour were examined. As demonstrated for Bar-tailed Godwits *Limosa lapponica*, the moult stage at stopover sites during spring migration can represent an honest fitness indicator. Birds with a more complete breeding plumage are heavier indicating a better physical condition (Piersma and Jukema 1993). This may also have important consequences for behavioural constraints during foraging. Heavier birds in good physical condition – indicated by a more complete breeding plumage – may be able to decrease their food intake and, consequently, are able to spend more time on vigilance, thereby decreasing predation risk. On the other hand, heavier, potentially more competitive birds may occupy better feeding habitats and, consequently, show higher food intake rates. This may be additionally enhanced by a bird's social status. Differences in male plumage colour are related to the social status which translates into different mating strategies of male Ruffs on the breeding grounds (Van Rhijn 1991). However, a high social status of males as indicated by their plumage coloration may also be advantageous for monopolizing better feeding sites at staging areas, thereby affecting feeding rate and vigilance.

Methods

Study area

The Seewinkel (47° 82' N, 16° 77' E, alt. 115m asl) located east of Lake Neusiedl at Burgenland, Eastern Austria is a stopover site of international importance for waders, particularly for Ruffs (Laber 2003). During spring migration Ruffs represent the most abundant wader species in the area with maximum numbers of more than 10,000 birds per day (Laber 2003; Kohler et al. 2009).

The study area is characterised by shallow soda ponds. These pools are shallow basins with a depth of about 30-50 cm (Wielander 2005) and some of them dry up nearly every year (Wolfram et al. 1999). They usually have extremely high pH values, ranging from pH 9 to pH 12, due to a high amount of carbonate (CO_3^{2-}) and bicarbonate ions (HCO_{3-}). When these ions combine with Na^+ ions, salts are formed (Krammer 2005). The dominant salt in the shallow soda ponds is Na_2CO_3 (Wolfram

1999). There are two types of salt pans: 'black water' and 'white water' lakes. Because of a high amount of humic substrates, black water lakes have reddish-brown colour. White water lakes are typically grey because of heavy wind action eroding fine sediment from the lake bottom (Wolfram 1999). Among these salt pans four have been chosen for this study: Darscho (D), Illmitzer Zicklacke (IZ), Neubruchlacke (N) and Oberer Stinkersee (OS) (Fig. 1). These selected locations were particularly suitable for this study because of an existing observation hut (at IZ) or good access by car (at D, N, OS).

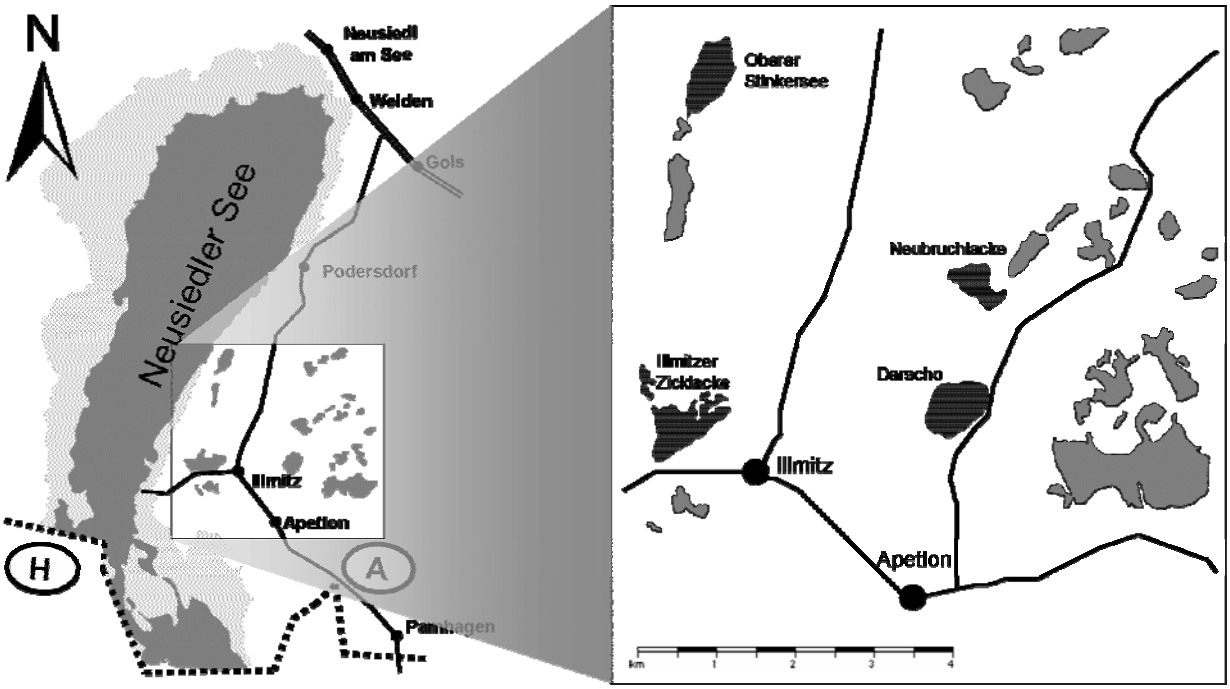

Fig. 1 Maps indicating location of study area (left figure) and study sites (right figure). The four study sites, where foraging Ruff were observed (Oberer Stinkersee, Illmitzer Zicklacke, Darscho and Neubruchlacke), are marked by darker fillings, other salt pan-areas are grey

Recording bird behaviour

Foraging behaviour of Ruffs was recorded with a digital handy cam (Panasonic HDC-SX5) from an observation hut or a car to get as close as possible to the birds without affecting their behaviour by the presence of the observer. Filming of individual birds, small flocks or parts of larger flocks lasted for at least one minute. Date and time were recorded automatically during filming by the digital hand cam. Additionally,

observation site and weather conditions – wind force (1: windless; 2: weak wind; 3: moderate wind; 4: strong wind) and cloud cover (1: no clouds; 2: moderate cloud cover; 3: closed or nearly closed cloud cover) – were noted. For bird flocks, additionally total flock size and – for mixed species flocks – the number of individuals per species were recorded. A bird flock was defined as a con- or heterospecific group of waders all within a distance of approximately 20 body lengths to a nearest neighbour.

Due to the large number of present Ruffs an individual was most likely not recoded more than once on consecutive days. In several instances information on foraging behaviour of Ruffs in larger flocks was recorded on more than one focal bird. However, the same individual was never recorded twice during the same session.

Field work was conducted from 1 April until 30 May 2008 (max. 5 days a week; total of 40 observation days). There was no field work on weekends and holidays due to the risk of higher anthropogenic disturbance potentially affecting foraging behaviour and feeding site selection of Ruffs. Furthermore, no field work was done during extremely bad weather conditions (e.g. heavy rain). Each salt pan was visited twice a day at an interval of three to four hours.

Analysis of film sequences

To quantify the frequency of scan and peck rate of foraging Ruffs, one 30 sec. film sequence of every film was selected during which the focal bird was not hidden by vegetation structures or other birds. Scan rates (quantified as number of scans per 30 sec) were used as measurement of vigilance. Scanning behaviour was defined as rising of the head from the head-down foraging position (0°) to a bill position of at least 80°. Peck rates (quantified as number of pecks per 30 sec) were used as measurement of food intake. Pecking was defined as touching or investigating the surface of water, soil or vegetation with the tip of the bill.

Beside this, three different moult stages were classified: prenuptial plumage with no signs of moult (1), first signs of moult (2) and moult proceeding into breeding plumage (3). In male Ruffs their social status is strongly related to plumage colouration (Van Rhijn 1991). In this study two categories of plumage colouration were distinguished: males with white coloured necks, which correspond to

submissive satellite males, and males with non-white coloured necks, representing dominant males (Van Rhijn 1991).

Two types of feeding habitats were defined: semi-aquatic (foraging in water) and terrestrial (foraging on land). Additionally, vegetation cover of foraging habitats was categorized as no or sparse, low vegetation (A) or dense, high vegetation reaching at least the bird's intertarsal articulation in height (B).

Data analysis

Effects of abiotic and biotic variables on foraging behaviour of feeding Ruffs were separately assessed for scan and peck rate by Generalized Linear Models (GLMs) using a log-link function. GLMs were calculated using all predictor variables and possible subsets. To identify which predictor variables had the strongest influence on scanning and pecking behaviour, models were ranked according to their information content as determined by Akaike's Information Criterion (AIC) (Crawley 1993; Burnham and Anderson 2002); best models have lowest AIC values. For all models within 4 AIC values of the best model (with lowest AIC), we calculated their AIC weights (Burnham and Anderson 2002). Higher AIC weights indicate a higher relative likelihood of a model compared with competing models (Wagenmakers and Farrell 2004). Wald statistics for the GLMs were used to detect univariate effects of variables on scan and peck rates of Ruffs. All analyses were carried out in Statistica version 7.1 (Statsoft, Inc. 2005).

Results

A total of 681 film sequences of foraging Ruffs were analyzed. In total only 53 other waders belonging to seven species (*Charadrius dubius*, *Ch. alexandrinus*, *Limosa limosa*, *Tringa totanus*, *T. glareola*, *Calidris alpina*, *Actitis hypoleuca*) were observed foraging together with Ruffs. The number of other waders was very weakly related to the size of Ruff flocks (Spearman rank correlation: $r_s = 0.09$, N = 472, $p = 0.042$). Due to the very small number of other waders observed mixing with Ruffs during foraging, they were not considered in all subsequent analyses and flock size was exclusively defined as the number of jointly foraging Ruffs.

The two main components of foraging behaviour, scan rate and peck rate, were not correlated (r = -0.05, N = 681, p = 0.205). Therefore, effects of biotic and abiotic predictor variables on both components of Ruffs´ foraging behaviour were analyzed separately.

Scan rate

Scan rate of Ruffs was negatively correlated with flock size (r = -0.59, N = 681, p < 0.001; Fig. 2). However, the remaining variability in scan rates of individual birds, which cannot be explained by varying flock sizes, is enormous indicating that other factors may influence vigilance.

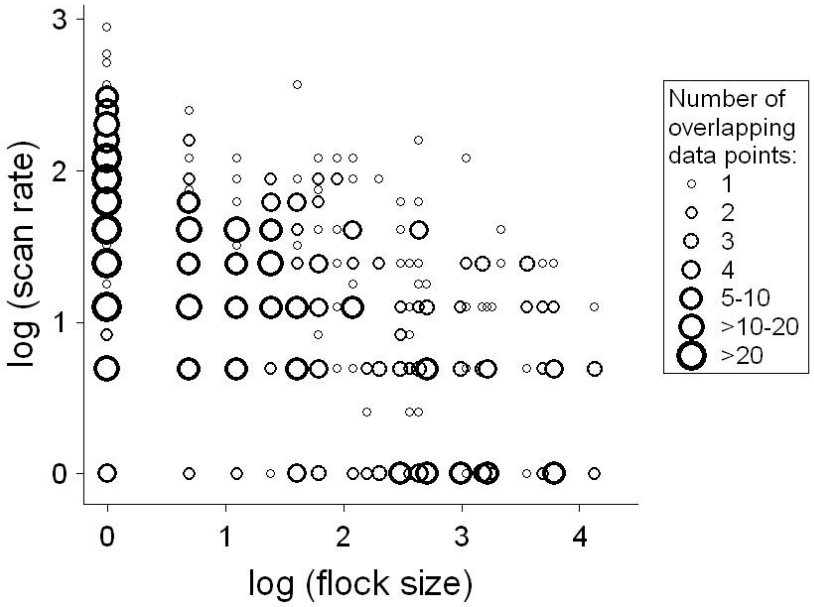

Fig. 2 Scan rates of Ruffs (N = 681) foraging individually or in flocks

To test which other variables affect scan rate of foraging Ruffs, GLMs were calculated including all variables and all possible subsets. Subsequently, models were ranked according to AIC. Of all predictor variables (location, vegetation cover, wind force, cloud cover, date, time, feeding habitat, flock size) tested for their effects on scan rate of Ruffs, six remained in the best model: location, feeding habitat, wind force, cloud cover, date and flock size (Table 1). Of these variables location, feeding habitat and flock size were included in all twelve best models. These three variables also proved to strongly affect Ruffs´ scan rates according to Wald statistics (Table 2).

Table 1 Akaike model selection for assessing effects of eight different variables on scan rates of foraging Ruffs. Presented GLMs represent all models within 4 AIC values of the model with the lowest AIC

Variables included	Df	AIC	ΔAIC	AIC weight
Location, feeding habitat, wind force, cloud cover, date, flock size	11	980.11	0.00	0.1990
Location, feeding habitat, wind force, cloud cover, date, time, flock size	12	981.38	1.27	0.1055
Location, feeding habitat, wind force, cloud cover, flock size	10	981.64	1.53	0.0926
Location, vegetation cover, feeding habitat, wind force, cloud cover, date, flock size	12	981.89	1.77	0.0820
Location, feeding habitat, cloud cover, date, flock size	8	981.92	1.81	0.0804
Location, feeding habitat, wind force, cloud cover, time, flock size	11	982.64	2.53	0.0560
Location, feeding habitat, cloud cover, date, time, flock size	9	983.15	3.04	0.0436
Location, vegetation cover, feeding habitat, wind force, cloud cover, date, time, flock size	13	983.24	3.13	0.0416
Location, vegetation cover, feeding habitat, wind force, cloud cover, flock size	11	983.46	3.35	0.0372
Location, vegetation cover, feeding habitat, cloud cover, date, flock size	9	983.52	3.41	0.0362
Location, feeding habitat, wind force, time, flock size	9	983.57	3.46	0.0353
Location, feeding habitat, wind force, flock size	8	983.86	3.75	0.0310

Table 2 Results of Wald statistics testing for effects of eight predictor variables (included in the GLMs; see Table 1) on scan rate of foraging Ruffs

Variable	Df	Wald statistic	*P*
Constant	1	185.24	<0.001
Location	3	90.16	<0.001
Vegetation cover	1	00.14	0.709
Feeding habitat	1	18.69	<0.001
Wind force	3	7.34	0.062
Cloud cover	2	7.30	0.026
Date	1	3.29	0.070
Time	1	0.66	0.4173
Flock size	1	87.70	<0.001

Scan rates of foraging Ruffs proved to be highest at the salt pan D and lowest at the sites IZ and N. Ruffs at OS showed an intermediate vigilance (Fig. 3a). Furthermore, terrestrially foraging Ruffs showed a significantly higher scan rate than semi-aquatic feeding birds (Fig. 3b). Flock size negatively affected scan rate (β = -0.362).

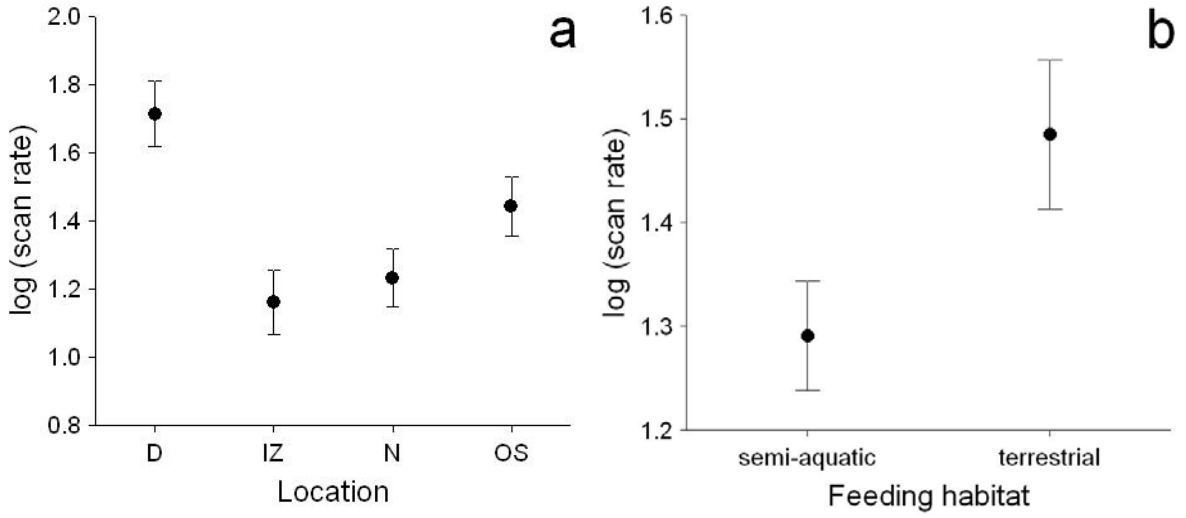

Fig. 3 Least squares means of scan rate (log transformed) ± 95% confidence interval for Ruffs at four different shallow saltwater lakes (D – Darscho, IZ – Illmitzer Zicklacke, N – Neubruchlacke, OS – Oberer Stinkersee) (a) and foraging in different habitats (b)

Peck rate and stepping rate

For analyzing which biotic and abiotic variables affect peck rate of foraging Ruffs, additionally to the eight predictor variables mentioned above, stepping rate was included as further explanatory variable. Stepping rate did decrease with increasing flock size (r_s = -0.32, N = 681, $p < 0.001$; Fig. 4). Furthermore, peck rate decreased with increasing stepping rate (r = -0.12, N = 681, p = 0.001; Fig. 5). However, calculated GLMs including all variables and possible subsets did neither indicate an important contribution of stepping rate nor flock size to explaining variance of peck rate.

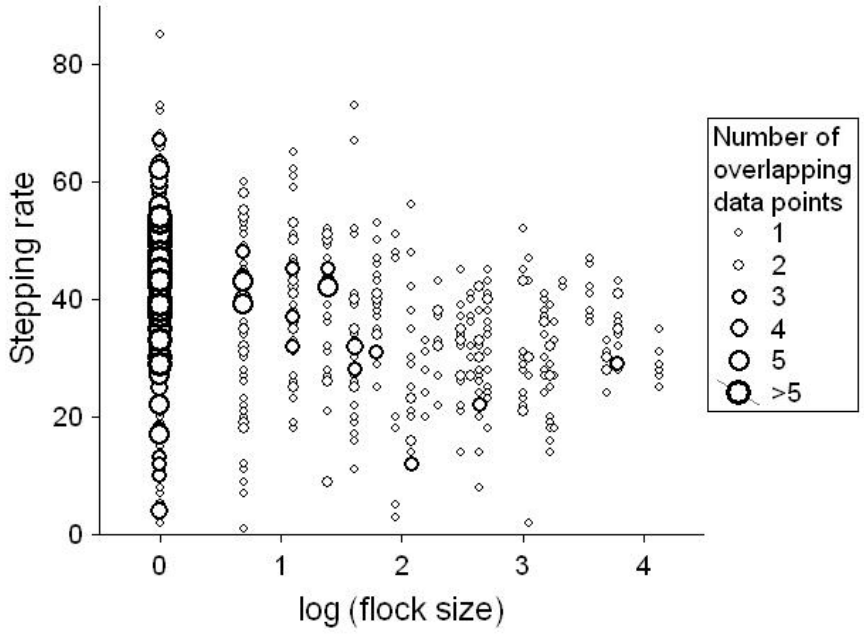

Fig. 4 Relationship between stepping rate and flock size in foraging Ruffs

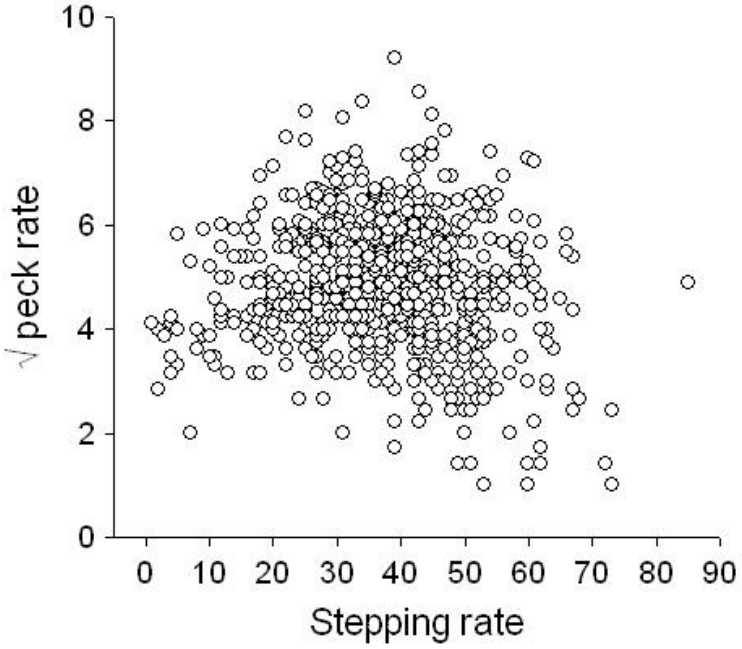

Fig. 5 Relationship between peck rate and stepping rate of foraging Ruffs

Four of nine variables remained in the best model: site, wind force, cloud cover and date (Table 3). Two of them, location and wind force, were included in all 23 best models and had a strong effect on peck rate according to Wald statistics (Table 4).

Table 3 Akaike model selection for assessing effects of nine different variables on peck rates of foraging Ruffs. Presented GLMs represent all models within 4 AIC values of the model with the lowest AIC

Variables included	Df	AIC	∆AIC	AIC weight
Location, wind force, cloud cover, date	9	2085.89	0.00	0.0890
Location, wind force, cloud cover, date, time	10	2087.32	1.43	0.0436
Location, feeding habitat, wind force, cloud cover, date	10	2087.37	1.48	0.0425
Location, wind force, cloud cover, date, stepping rate	10	2087.60	1.71	0.0380
Location, wind force, cloud cover, date, flock size	10	2087.81	1.92	0.0341
Location, vegetation cover, wind force, cloud cover, date	10	2087.83	1.93	0.0339
Location, wind force, cloud cover	8	2088.31	2.41	0.0266
Location, feeding habitat, wind force, cloud cover, date, stepping rate	11	2088.78	2.89	0.0210
Location, feeding habitat, wind force, cloud cover, date, time	11	2088.81	2.92	0.0207
Location, wind force, cloud cover, date, time, stepping rate	11	2089.02	3.12	0.0187
Location, wind force, cloud cover, date, time, flock size	11	2089.08	3.19	0.0180
Location, wind force	6	2089.09	3.19	0.0180
Location, vegetation cover, wind force, cloud cover, date, time	11	2089.13	3.24	0.0176
Location, vegetation cover, feeding habitat, wind force, cloud cover, date	11	2089.22	3.32	0.0169
Location, feeding habitat, wind force, cloud cover, date, flock size	11	2089.33	3.44	0.0160
Location, wind force, cloud cover, flock size	9	2089.35	3.46	0.0158
Location, wind force, cloud cover, stepping rate	9	2089.49	3.60	0.0147
Location, vegetation cover, wind force, cloud cover, date, stepping rate	11	2089.55	3.65	0.0143
Location, wind force, cloud cover, date, flock size, stepping rate	11	2089.56	3.67	0.0142
Location, wind force, date	7	2089.66	3.76	0.0136
Location, vegetation cover, wind force, cloud cover, date, flock size	11	2089.74	3.84	0.0130
Location, feeding habitat, wind force, cloud cover	9	2089.83	3.94	0.0124
Location, wind force, cloud cover, time	9	2089.86	3.97	0.0122

Table 4 Results of Wald statistics testing for effects of nine predictor variables (included in the GLMs; see Table 3) on peck rate of foraging Ruffs

Variable	Df	Wald statistic	*P*
Constant	1	1072.39	<0.001
Location	3	111.85	<0.001
Vegetation cover	1	0.33	0.5660
Feeding habitat	1	0.83	0.3626
Wind force	3	12.81	0.0051
Cloud cover	2	7.42	0.0245
Date	1	3.13	0.0767
Time	1	0.81	0.3670
Flock size	1	0.08	0.7838
Stepping rate	1	0.43	0.5103

Highest peck rates of foraging Ruffs were recorded at site OS, lowest rates at N. Ruffs feeding at the two salt pans D and IZ showed intermediate peck rates (Fig. 6a). Ruffs appeared to adapt their feeding behaviour to changes in wind force. Our data show an increasing peck rate with increasing wind force (Fig. 6b).

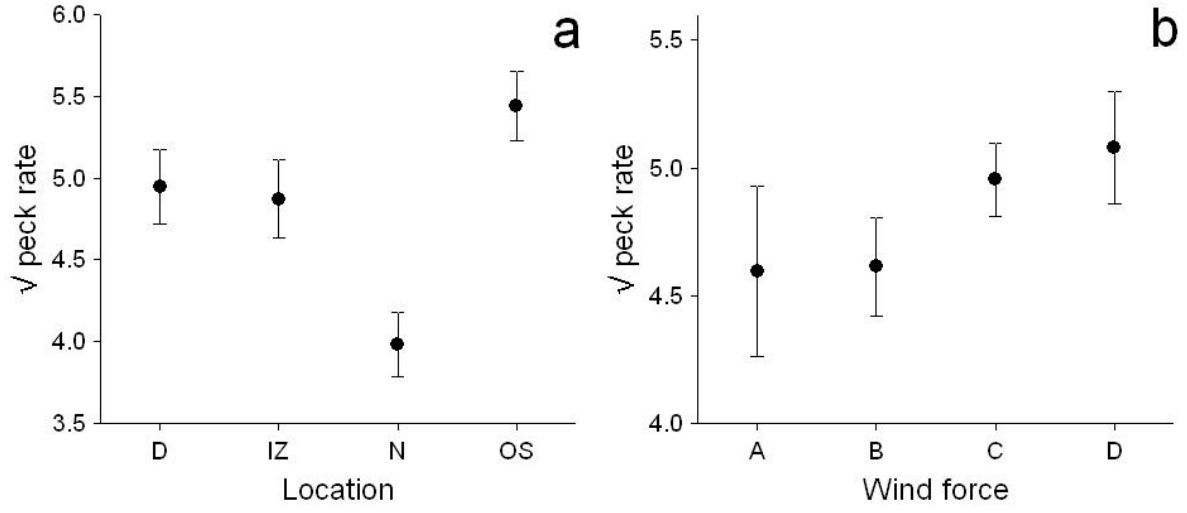

Fig. 6 Least squares means of peck rate (square root transformed) ± 95% confidence interval for Ruffs foraging at four different salt pans (D – Darscho, IZ – Illmitzer Zicklacke, N – Neubruchlacke, OS – Oberer Stinkersee) and (a) exposed to different wind forces (b)

Effects of moult stage and male plumage on foraging behaviour

Scan rate and peck rate of Ruffs differed significantly between birds in different moult stages (one-way ANOVAs; scan rate: $F_{2,574}$ = 6.11, p = 0.002; peck rate: $F_{2,574}$ = 9.40, p < 0.001). Birds in prenuptial plumage were less vigilant than moulting birds (Fig. 7a) and mean peck rate was significantly lower in birds with first signs of moult compared to birds with prenuptial plumage and birds in a later stage of moulting (Fig. 7b).

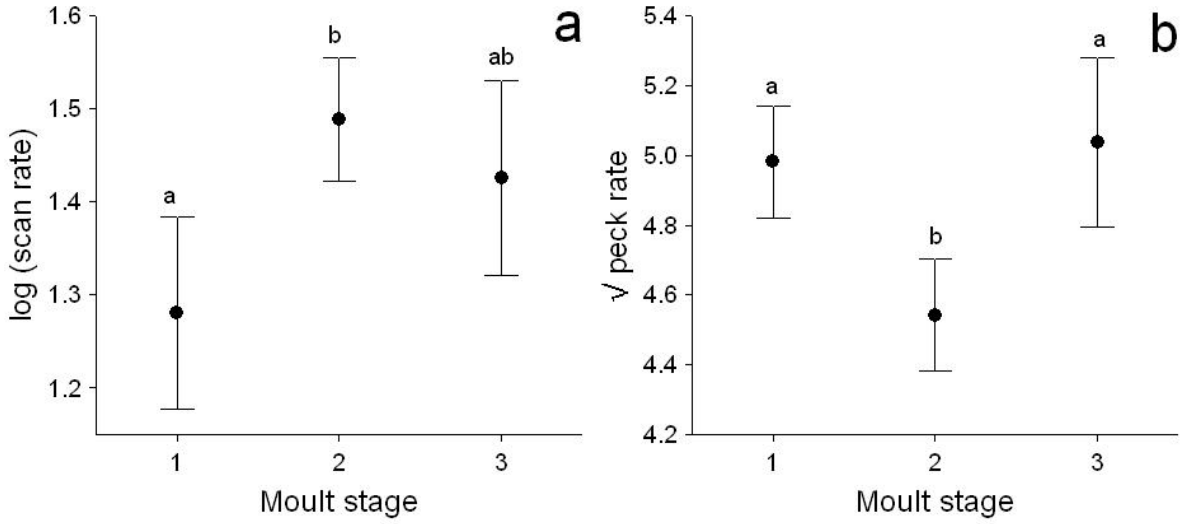

Fig. 7 Mean scan rate (a) and peck rate (b) ± 95% confidence interval of Ruffs in different moult stages: 1 – prenuptial plumage (N = 180), 2 – first signs of moult (N = 258), 3 – moulting (N = 139). Different letters indicate significant differences (Tukeys Honest Significant Difference-Test; p < 0.05)

However, differences of scan and peck rates between moult stages may be caused by other variables than moult as the proportion of randomly selected focal birds belonging to different moult stages differed significantly between decades (Chi-square test: χ^2 = 134.02, df = 6, p < 0.001). The relative abundance of prenuptial birds decreased with progressing spring migration until the end of April and then increased again in the first decade of May (Fig. 8). Hence, we calculated GLMs assessing separately effects of moult stage on vigilance and food intake. The models only included all abiotic and biotic predictor variables that already proved (see above) to have a significant effect on scan and/or peck rate (location, feeding habitat, flock size, cloud cover, wind force). Furthermore, we included date as predictor variable and allowed for a two-way interaction between date and moult stage. The variable

moult stage was only included two of the nine best models assessing effects on vigilance (Appendix Table A1) and in one of eight best models assessing effects on food intake (Appendix Table A3). According to Wald statistics moult stage did not contribute significantly to explain variance of vigilance level (Appendix Table A2) and peck rate (Appendix Table A4).

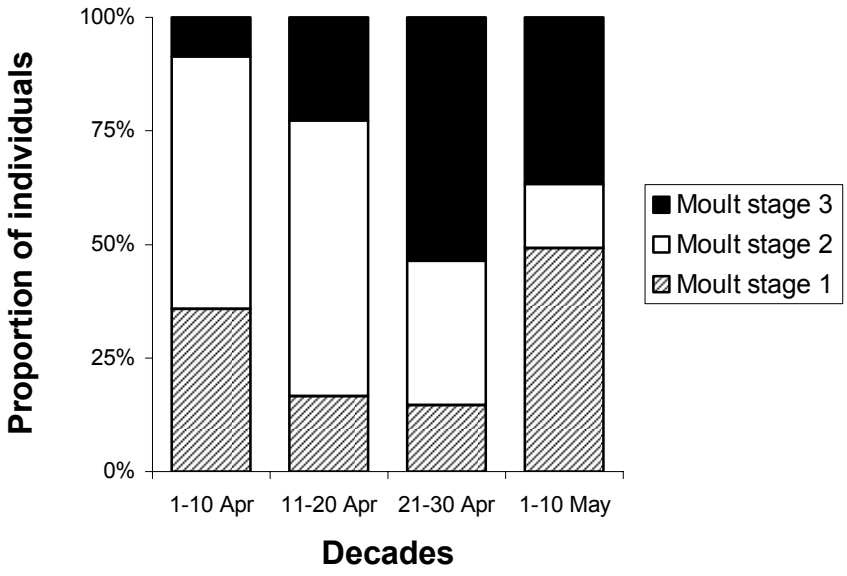

Fig. 8 Proportion of Ruffs in three different moult stages during spring migration. Moult stages: 1 – prenuptial plumage, 2 – first signs of moult, 3 – moulting. $N_{1\text{-}10\ April} = 243$, $N_{11\text{-}10\ April} = 132$, $N_{21\text{-}30\ April} = 82$, $N_{1\text{-}10\ May} = 120$

Scan rate differed significantly between male colour morphs (t test: $t = -2.72$, df = 164, $p = 0.007$). The mean vigilance level of white necked Ruffs was lower than of Ruffs belonging to other plumage colour morphs (Fig. 9a). Peck rate was slightly lower in white morph males (Fig. 9b), but the difference did not achieve significance ($t = -1.73$, df = 164, $p = 0.084$). However, the proportion of male Ruffs with different neck plumage colour differed significantly between decades (Chi-square test: $\chi^2 = 15.14$, df = 3, $p < 0.002$). While white-necked Ruffs still represented the dominant male colour morph in the first decade of April, their proportion rapidly decreased below 50% with progressing season (Fig. 10). Therefore, other variables than social status may be more important for explaining differences in scan and peck rate between white and non-white necked male Ruffs.

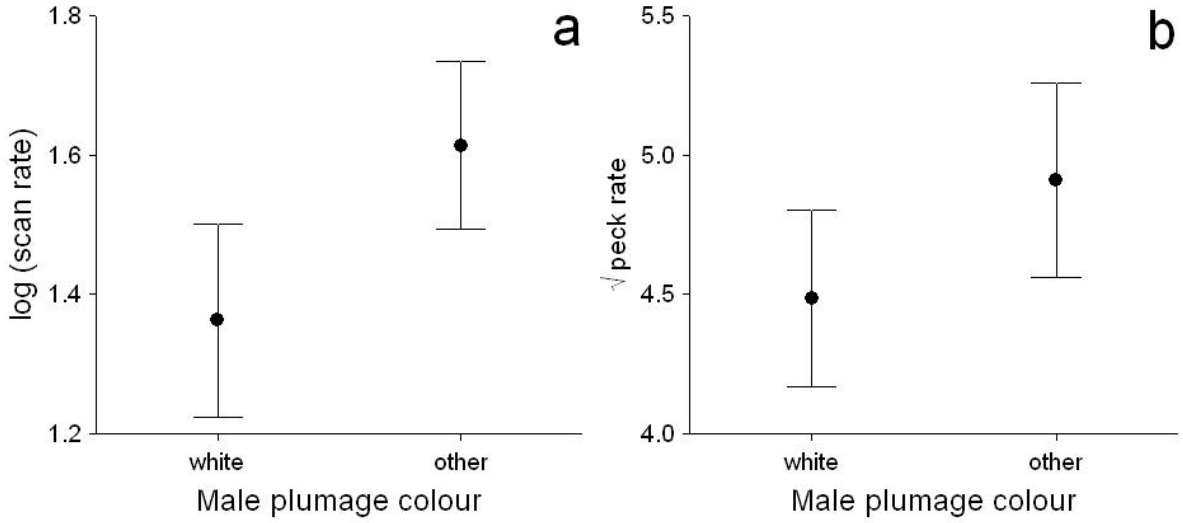

Fig. 9 Mean scan rate (a) and peck rate (b) ± 95% confidence interval of foraging Ruffs with white (N = 72) and non-white neck and head plumage colour (N = 94). Only scan rate but not peck rate differed significantly between colour morphs (see text)

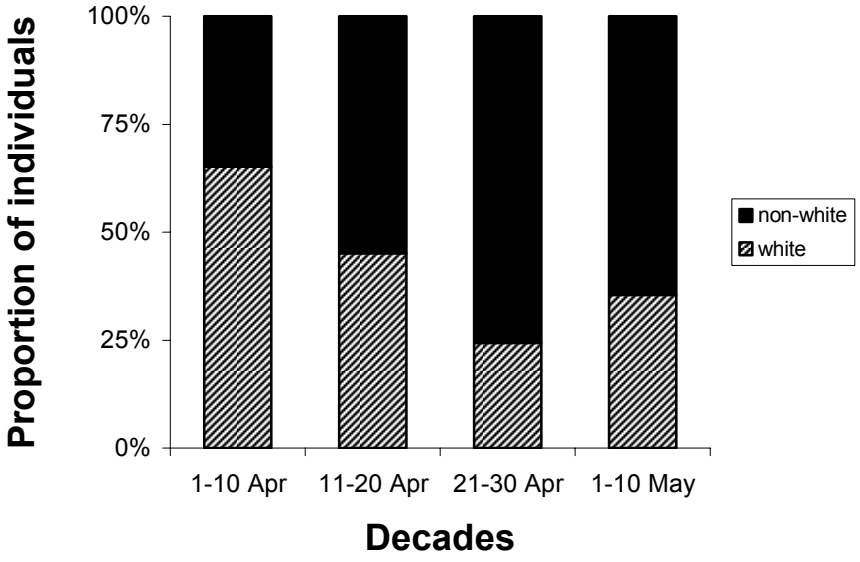

Fig. 10 Proportion of male Ruffs with white and non-white neck plumage colouration with progressing spring migration. $N_{1\text{-}10\ April}$ = 43, $N_{11\text{-}10\ April}$ = 51, $N_{21\text{-}30\ April}$ = 41, $N_{1\text{-}10\ May}$ = 31

We calculated GLMs including the same variables as the models used to assess effects of moult stage on vigilance and food intake, but replaced the variable moult stage by the variable male neck colour morph. The variable male colour morph was only included in five of the nine best models assessing effects on vigilance (Appendix Table A5). Although male plumage colour was included as predictor variable in a substantial proportion of the 73 best models assessing effects on food

intake (Appendix Table A7), Wald statistics did not indicate any significant contribution of male colour morph to neither vigilance level (Appendix Table A6) nor peck rate (Appendix Table A8).

Discussion

Trade-off between vigilance and food intake?

Vigilance is expected to decline with increasing food intake rate when animals face time constraints on foraging (McNamara and Houston 1992). In contradiction, it is often assumed that an increase in vigilance, e.g. in response to increased predation risk, translates into a decrease in food intake (Pulliam 1973; Fritz et al. 2002) because a bird cannot peck for food and raises it head to scan for predators at the same time (Slotow and Rothstein 1995a). An increase in vigilance can have a direct negative effect on the food intake rate through a reduction in the time available for feeding or through a decrease in foraging efficiency (Lima and Dill 1990). However, Cresswell et al. (2003) demonstrated that pecking and vigilance do not always have to be mutually exclusive. Chaffinches (*Fringilla coelebs*) with higher peck rates responded more quickly to a model Sparrowhawk flying nearby. This may also partly explain why no correlation between scan and peck rates were found in Ruffs by this study. Also others studies showed little evidence supporting a trade-off of peck rate against scan rate (e.g. Slotow and Rothstein 1995a).

Scan rate

In this study, as expected, flock size had a strong effect on scan rate: vigilance level decreased with increasing flock size. A reduction in individual vigilance with an increase in group size is one of the most frequently reported relationships in the study of bird behaviour (Arenz 2003; but: Catterall et al. 1992; Pöysä 1994; Slotow and Rothstein 1995a; Slotow and Coumi 2000). It is usually interpreted as a response to the lower risk of predation in larger groups (Beauchamp 2003a). However, it was emphasized that a decline of vigilance in individual birds may not be a direct consequence of an increase in group size because group size can be confounded by other ecological factors (Roberts 1996; Arenz 2003; Beauchamp

2009). For example, the likelihood that the group will contain an individual at high risk of capture, if an attack should occur, may increase with increasing group size (Arenz 2003). Furthermore, in larger groups interference among foragers increase, what in turn leads to an enhanced scramble for limited resources and as a consequence foragers adopt more risky behavioural pattern like investing less time in vigilance in response to higher competition (Beauchamp 2003a). Moreover, a lower vigilance could be partly due to the stimulation of feeding in groups and a higher effort to coordinate activities within a group (Beauchamp 2003b). Furthermore, larger groups can aggregate at sites with better food quality and/or higher food density (Beauchamp 2009). Consequently, individual birds may spend more time on feeding and less time on scanning when feeding is incompatible with vigilance (Roberts 1996; Beauchamp 2009). This may be particularly the case in species such as the Ruff, which handle food with their head down, a posture not entirely compatible with vigilance (Lima and Bednekoff 1999).

Another theory considering food density predicts that in areas of low food availability birds are more vigilant to glean information about richer food patches through the behaviour of other group members. However, such a relationship may only apply to species foraging on heterogeneous, patchily distributed resources (Beauchamp 2009). Although food density was not measured in our study, it appears to be unlikely that food exploited by Ruffs in the relatively uniform water-land transition zone of salt pans is so heterogeneously distributed that it affects vigilance of birds on a small scale at individual locations.

Social vigilance should also increase as scrounging opportunities become available (Beauchamp 2009). However, scrounging only should be a relevant factor when food availability is a limiting factor which appears to be unlikely in the water-transition zone of salt pants. Furthermore, neither aggressive interaction between Ruffs indicating competition nor scrounging was observed during our study.

Although a large amount of variation remains unexplained in studies testing for effects of group size on vigilance (Beauchamp 2008), there is clear evidence for a direct relationship between group size and vigilance when controlled for other potentially confounding variables (Roberts 1996; Beauchamp 2009). For example, a study on effects of several variables (time of day, human disturbance, precipitation, distance from cover, temperature and flock size) on vigilance of American Crows *Corvus brachyrhynchus* demonstrated that flock size accounted for most of the

variability in vigilance (Ward and Low 1997). Also in our study flock size remained as one important variable affecting scan rate, even when controlled for other important variables such as location and feeding habitat.

Also disturbance through human attendance can be a reason for showing increased alertness at feeding sites (Sirot 2006). For example, a wintering population of Brent Geese *Branta b. bernicla* spent less time feeding but more time vigilant on days when human disturbance was high. At the same time disturbance also clearly increased flight time of the geese, accompanied by an increased energy expenditure (increase of hourly energy expenditure up to 38.5%) (Riddington et al. 1996). Human disturbance could be also one reason for the observed differences of scan rates of foraging Ruffs at the four studied salt pans at Seewinkel. Scan rates were highest at Darscho, a salt pan, which is situated right beside a main road and a bike path. Here, bathers, riders and photographers were frequently observed during the field work for this study. In contrast the southern bank of the Illmitzer Zicklacke and the Neubruchlacke were less disturbed and Ruffs showed lower vigilance levels compared to the other two salt pans.

Differing predation risk with respect to location is considered to be a key influence on many aspects of bird behaviour such as the choice of feeding patches (Lima et al. 1999). For species that rely on detecting predators by sight, increased visual obstruction has been shown to increase vigilance. For example, Chaffinches *Fringilla coelebs* (Whittingham and Evans 2004) foraging on artificially created stubble substrates raised their vigilance levels by 13% when foraging in obstructed patches (long stubble 13 cm tall), as compared with patches offering a clear field of view (short stubble 3 cm tall). Additionally predator detection was 24 % slower in obstructed patches than in patches with a clear field of view. Another important point about habitat structure and foraging is the way in which birds perceive cover (Whittingham and Evans 2004). Proximity to cover can have two effects on a prey animal: it can provide a hiding place and protection from an attack, but it can also obstruct their view of approaching predators (Lazarus and Symonds 1992). Species like the Grey Partridge *Perdix perdix* and the Corncrake *Crex crex* use their feeding habitats also as a protective cover and therefore they show a tendency to delay escape flight when a predator approaches; they remain still and rely on crypsis (Whittingham and Evans 2004). Such species benefit from vegetation cover. However, vigilance rate of birds can also remain unchanged with increasing distance

to cover (e.g. Lima 1988; Slotow and Rothstein 1995a) or can even increase (e.g. Caraco et al. 1980b; Hogstad 1988). In our study on Ruffs, which in most cases escape from approaching predators like hawks through rapid flight manoeuvres, trying to reach as fast as possible a greater flying height than the attackers (Scheufler and Stiefel 1985), proximity to cover appeared to increase scan rates. Ruffs feeding in terrestrial habitats – usually closer to vegetation cover such as reed beds, bushes, or trees – had a higher vigilance level than individuals foraging in semi-aquatic habitats of the open salt pans, perhaps in order to compensate for higher predation risk due to predators attacking waders from nearby vegetation cover. A higher predation risk close to cover was recorded for Redshanks *Tringa totanus*. Individuals feeding on the strandline, close to cover, entailed a much higher risk of being attacked by Sparrowhawks *Accipiter nisus* and of the attack being successful (Whitfield 2003). The importance of vegetation cover is also emphasized by the observation that ground-foraging songbirds decrease their vigilance rate with distance from cover (Lima 1987; Slotow and Rothstein 1995a).

We are aware that vigilance of birds foraging in groups also is affected by group geometry and a bird's position within the flock (Arenz 2003). Usually, vigilance is higher in individuals at the edge of a flock (Randler 2005; Dias 2006). However, in Ruffs foraging at the shoreline of salt pans at Seewinkel, the spatial organization of flocks is more or less a chain of birds foraging along the water-land transition zone. Such groups do not have a well developed "centre" and "margin" as, for example, wader flocks foraging on extensive mudflats. Therefore, in our study only birds at the two outer edges of the flocks might have been faced a slightly higher predation risk resulting in a vigilance level deviating from the mean scanning rates of birds in the respective group.

Waders can "share" vigilance with other wader species, but the extent of sharing information depends on the relative size of the species joining mixed flocks (Metcalfe 1984). Due to the very low number of other waders observed mixing with foraging Ruffs, we do not expect that they contributed much to the variance of Ruffs´ vigilance level, particularly because many of them were much smaller than Ruffs (e.g. *Charadrius* species, *Calidris alpina*, *Actitis hypoleuca*).

Our study did not take into consideration the distance between focal birds and foraging neighbours. Neighbour distance can explain a substantial proportion of

variance in birds´ vigilance levels as documented for foraging Red-billed Choughs *Pyrrhocorax pyrrhocorax* (Rolando et al. 2001).

Peck rate

Also in peck rate an influence of flock size is often assumed. Birds in larger flocks can spend more time foraging (Dias 2006; Sansom et al. 2008). However, this does not appear to translate necessarily into a foraging benefit. For example, in foraging Redshanks food intake was not related to flock size (Sansom et al. 2008). Principally, the relationship between mean food intake rate and group size can take on four different shapes (Beauchamp 1998). Most commonly mean food intake rate increases with group size (Beauchamp 1998). For example, peck rate can increase with group size because time needed to locate food patches can be reduced (Beauchamp et al. 1997) and as a consequence more time can be allocated to foraging. Conversely, mean food intake rate can decrease with group size because of increasing aggressive interactions, which can decrease individuals´ foraging time and lower food intake in larger groups (Moody and Ruxton 1996; Stillman et al. 1997). Or the relationship can be a combination of the two relationships mentioned before. Then mean food intake first increases to a maximum and then decreases with group size, a relationship that could be found in foraging White-winged Crossbills *Loxia leucoptera* (Slotow and Rothstein 1995a; Benkman 1997).

In our study food intake rate was not directly related to group size, which was also reported by other studies (e.g. Rolando et al. 1997). However, our data show that stepping rate decreased with increasing flock size, which is contrary to the expectation that flock size increases competition and, therefore, increases stepping rate because birds have to search more intensively for food. The decreased stepping rate of Ruffs in larger flocks, as found in our study, indicates better food availability at sites with larger aggregations of feeding birds. This is underlined by the observation that food intake increased with decreasing stepping rate.

Food intake rates recorded in our study differed significantly between salt pans. Peck rate was highest at Oberer Stinkersee, intermediate at Darscho and Illmitzer Zicklacke and lowest at Neubruchlacke. This may reflect different prey availability levels at our four study sites.

As Ruffs are mainly visual foragers (Glutz von Blotzheim et al. 1975) it did not come as a surprise that wind force had an influence on peck rate. Wind can produce strong wave action, which in turn stirs up sediments and clouds the sight for prey (Evans 1976). Furthermore birds which feed with their heads above the water surface have to overcome the problem of the change in refractive index between air and water, which leads to distortion of the location of potential prey (Evans 1976). This problem is augmented by wind action, which makes the water surface more turbulent (Evans 1976). The influence of wind force could be observed on a colour-marked Grey Plover (*Pluvialis squatarola*), which fed on the same site at the same time at two different days. On the less windy day (wind force: 8 m/sec) the bird made an average of 3.9 attempts to take prey each minute, and 47 % were successful. On the windier day (13-20 m/sec) the peck rate was only 1.9 each minute, and only 39 % were successful (Evans 1976). Perhaps, Ruffs foraging in salt lakes at Seewinkel showed higher peck rates during periods of stronger wind because they had to compensate for a smaller proportion of successful feeding attempts.

In Ruffs time constraints most likely will become more important during spring migration when breeding season is approaching and they have to speed up their migration to reach their breeding grounds. Under such circumstances they may have to shorten their stopover duration at staging sites and, consequently, have to increase their food intake rate to deposit enough energy before continuing their northward migration. Indeed the factor date remained in the best GLMs testing for effects of extrinsic and intrinsic predictor variables on peck rate. However, peck rate only increased slightly towards the end of our observation period perhaps indicating that time constraints do not have a prominent effect on foraging in Ruffs at staging sites during spring migration.

Effects of moult stage on foraging behaviour

Adult male Ruffs moult three times a year. The post-breeding moult during summer and autumn involves the whole plumage and produces the non-breeding plumage. The winter moult involves most of the plumage (but not the large flight-feathers) and produces the prenuptial plumage. The third moult is the pre-breeding moult during early spring, involving head, breast and many small body-feathers, producing the nuptial plumage (Van Rhijn 1991). Pre-breeding moult predominantly takes place

between the middle of March and the middle of April (Glutz von Blotzheim et al. 1975), what goes along with the observed proportion of individuals at Seewinkel. That our data showed an increase of the number of prenuptial birds at the beginning of May could indicate a higher proportion of Reeves, which usually depart from breeding grounds one month later than males (Delany et al. 2009). However, a reliable identification of sexes could not always be achieved. In adult females winter moult and pre-breeding moult merge into one another, and cannot be considered as separate processes (Van Rhijn 1991). At this stage of moult the plumage of Reeves looks very similar to the prenuptial plumage of males. Also the body size of Ruffs – with males being in most cases clearly larger than females (Van Rhijn, 1991) – often is not useful for field determination of sexes, particularly when birds are foraging alone. Due to these problems of sex determination in the field, sexes were not taken into account as predictor variable in analysing foraging behaviour of Ruffs.

Quality and colour of male nuptial plumage have shown to influence females' mate choice decisions (Höglund et al. 1990). Moult generally requires sufficient energy investment and the fact that shorebirds moult while also depositing energy stores for long-distance flights (Zwarts et al. 1990), suggests that nutrient storage and feather production can be compatible (Piersma and Jukema, 1993). But time- and energy-availability at stopover sites represent critical constraints on the occurrence of moult (Piersma and Jukema 1993). In Bar-tailed Godwits, a more complete breeding plumage is indicating a better physical condition (Piersma and Jukema 1993). Birds in a better physical condition may be more competitive and consequently may be capable to occupy better feeding habitats, thereby increasing their food intake rates. On the other hand, birds in better physical condition may be able to spend more time on vigilance. Indeed, our data showed that birds in a more complete breeding plumage, which may indicate a better physical condition, had an increased vigilance level. However, no clear effects of moult stage on peck or scan rates remained when controlled for other important variables influencing food intake rate and vigilance.

Effects of male plumage on foraging behaviour

Their high social status can give dominant individuals better access to high-quality feeding sites (e.g. Slotow and Rothstein 1995b), which, presumably, increases food

intake (e.g. Poysa 1988). However, there is little evidence in birds supporting that dominant individuals have higher food intake rates than subordinates (e.g. Slotow and Rothstein 1995a; Desrochers 1989).

Differences in plumage colour of male Ruffs are strongly linked to their social status (Van Rhijn 1991). The so called resident males, having mainly dark coloured ruffs and head-tufts, defend small mating territories (residences) on courtship areas (leks). Incidental or irregular visitors at the border of leks are called marginal males. They also have mainly dark coloured ruffs and head-tufts, do not defend residences and only occasionally show aggressive behaviour. These individuals may obtain the status of resident males during another phase of their life. Conversely, resident males can become marginal males. Resident and marginal males have been classified as independent males. Quite distinct from the independent males are the satellites, having mainly white or light coloured ruffs and head-tufts. They behave submissively towards the dominant resident males. The status of independent and satellite males is not interchangeable (Van Rhijn 1991).

On migration subordinate status could be a serious handicap to the deposition of energy stores (Piper and Wiley 1990), especially when food becomes scare or when the density of migrants increases (Woodrey 2000). Socially dominant migrants can gain an advantage in food acquisition, which can translate into an increased rate of fat deposition and a shorter length of stopover (Moore et al. 2003). However, the social status of male Ruffs does not seem to affect foraging behaviour. In their breeding areas independent and satellite males use the same feeding grounds without showing any aggressive behaviour (Scheufler and Stiefel 1985). Although our data indicated an increased scan rate and slightly higher peck rate of independent males, no significant effect of their social status on vigilance or food intake remained when other variables important for shaping foraging behaviour were considered.

Conclusions

Our data clearly showed that beside flock size, several other variables, particularly location, feeding habitat and weather conditions strongly affected vigilance and food intake of Ruffs foraging at salt pans at Seewinkel. Different scan rates at the four salt lakes may have been the result of different levels of human disturbance. Birds can loose much feeding time and energy when disturbed during foraging (Riddington et

al. 1996). Hence, disturbance can dramatically affect birds' survival if they do not have access to alternative feeding sites (Gill et al. 2001). Differences of peck rates between feeding locations may have been the result of salt lake specific differences in food supply. Substrate characteristics and the abundance of macrophytes seem to determine seasonal and spatial differences in abundance of benthic invertebrates in the salt pans at Seewinkel (Wolfram et al. 1999). Due to the spatio-temporal dynamic of food availability and human disturbance different salt pans at Seewinkel are not redundant as stopover sites for migrating waders, but may complement each other. Therefore, the protection of the existing salt pans may be an important precondition for maintaining the high conservation status of the Seewinkel as important stopover site for Ruffs and other waders in a long term. While in the year 1850 still around 139 salt pans (3,615 ha) existed, in 1957 only 79 salt pans (1,360 ha) remained with an ongoing decrease leading to a total of only 40 salt pans in the 1990s (Kohler et al. 1994). When the number of salt pans will further decrease, the conservation value of Seewinkel as important staging site for migrating wader will most certainly significantly decline in the near future.

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Appendix

Table A1 Akaike model selection for assessing effects of seven different variables (location, feeding habitat, wind force, cloud cover, date, flock size, moult stage) and the interaction moult stage x date on scan rates of foraging Ruffs. Presented GLMs represent all models within 4 AIC values of the model with the lowest AIC

Variables included	Df	AIC	∆AIC	AIC weight
Location, feeding habitat, cloud cover, date, flock size	8	812.98	0.00	0.2157
Location, feeding habitat, cloud cover, flock size	7	813.40	0.42	0.1749
Location, feeding habitat, cloud cover, flock size, moult stage x date	9	814.66	1.68	0.0931
Location, feeding habitat, wind force, cloud cover, flock size	10	814.74	1.76	0.0895
Location, feeding habitat, cloud cover, date, flock size, moult stage x date	10	814.77	1.79	0.0881
Location, feeding habitat, wind force, cloud cover, date, flock size	11	815.27	2.29	0.0687
Location, feeding habitat, cloud cover, flock size, moult stage	9	816.11	3.13	0.0450
Location, feeding habitat, cloud cover, date, flock size, moult stage	10	816.22	3.24	0.0426
Location, feeding habitat, wind force, cloud cover, flock size, moult stage x date	12	816.45	3.47	0.0380

Table A2 Results of Wald statistics testing for effects of seven predictor variables (included in the GLMs; see Table A1) on scan rate of foraging Ruffs

Variable	Df	Wald statistic	*P*
Constant	1	205.13	<0.001
Location	3	81.02	<0.001
Moult stage	2	0.98	0.612
Feeding habitat	1	16.62	<0.001
Wind force	3	3.29	0.349
Cloud cover	2	8.31	0.016
Date	1	1.36	0.243
Flock size	1	52.84	<0.001
Moult stage x date	2	2.40	0.302

Table A3 Akaike model selection for assessing effects of seven different variables (location, feeding habitat, wind force, cloud cover, date, flock size, moult stage) and the interaction moult stage x date on peck rates of foraging Ruffs. Presented GLMs represent all models within 4 AIC values of the model with the lowest AIC

Variables included	Df	AIC	∆AIC	AIC weight
Location	3	1333.376	0.00	0.1375
Location, flock size	4	1334.311	0.94	0.0861
Location, feeding habitat	4	1335.247	1.87	0.0539
Location, date	4	1335.319	1.94	0.0520
Location, cloud cover	5	1335.755	2.38	0.0418
Location, feeding habitat, flock size	5	1336.232	2.86	0.0330
Location, moult stage x date	5	1336.288	2.91	0.0320
Location, date, flock size	5	1336.301	2.93	0.0318
Location, wind force	6	1336.422	3.05	0.0300
Location, cloud cover, flock size	6	1336.535	3.16	0.0283
Location, moult stage	5	1336.614	3.24	0.0272
Location, cloud cover, date	6	1337.087	3.71	0.0215
Location, feeding mode, date	5	1337.174	3.80	0.0206

Table A4 Results of Wald statistics testing for effects of seven predictor variables (included in the GLMs; see Table A3) on peck rate of foraging Ruffs

Variable	Df	Wald statistic	*P*
Constant	1	2297.92	<0.001
Location	3	112.30	<0.001
Moult stage	2	0.22	0.898
Feeding habitat	1	0.30	0.587
Wind force	3	7.81	0.050
Cloud cover	2	11.12	0.004
Date	1	3.31	0.069
Flock size	1	0.68	0.410
Moult stage x date	2	0.25	0.883

Table A5 Akaike model selection for assessing effects of seven different variables (location, feeding habitat, wind force, cloud cover, date, flock size, male plumage morph) and the interaction male plumage morph x date on scan rates of foraging Ruffs. Presented GLMs represent all models within 4 AIC values of the model with the lowest AIC

Variables included	Df	AIC	ΔAIC	AIC weight
Location, male plumage morph, feeding habitat, flock size	6	228.29	0.00	0.1779
Location, feeding habitat, flock size	5	228.30	0.02	0.1763
Location, male plumage morph, feeding habitat, flock size, male plumage morph x date	7	229.02	0.73	0.1232
Location, feeding habitat, flock size, male plumage morph x date	6	229.80	1.51	0.0835
Location, feeding habitat, date, flock size	6	230.09	1.80	0.0723
Location, male plumage morph, feeding habitat, date, flock size	7	230.22	1.93	0.0677
Location, male plumage morph, feeding habitat, date, flock size, male plumage morph x date	8	230.99	2.70	0.0461
Location, feeding habitat, cloud cover, flock size	7	231.59	3.30	0.0342
Location, male plumage morph, feeding habitat, cloud cover, flock size	8	231.75	3.46	0.0315

Table A6 Results of Wald statistics testing for effects of seven predictor variables (included in the GLMs; see Table A5) on scan rate of foraging Ruffs

Variable	Df	Wald statistic	*P*
Constant	1	53.33	<0.001
Location	3	37.30	<0.001
Male plumage morph	1	1.81	0.179
Feeding habitat	1	10.80	0.001
Wind force	3	0.85	0.837
Cloud cover	2	0.75	0.687
Date	1	0.02	0.890
Flock size	1	16.13	<0.001
Male plumage morph x date	1	0.77	0.382

Table A7 Akaike model selection for assessing effects of seven different variables (location, feeding habitat, wind force, cloud cover, date, flock size, male plumage morph) and the interaction male plumage morph x date on peck rates of foraging Ruffs. Presented GLMs represent all models within 4 AIC values of the model with the lowest AIC

Variables included	Df	AIC	ΔAIC	AIC weight
Location, male plumage morph, wind force	7	572.50	0.00	0.0356
Location	3	572.54	0.05	0.0348
Location, wind force, male plumage morph x date	7	572.99	0.50	0.0278
Location, male plumage morph	4	573.01	0.51	0.0276
Location, male plumage morph x date	4	573.12	0.62	0.0261
Location, cloud cover	5	573.25	0.75	0.0244
Location, male plumage morph, wind force, cloud cover	9	573.34	0.84	0.0234
Location, male plumage morph, cloud cover	6	573.40	0.91	0.0226
Location, wind force	6	573.44	0.95	0.0222
Location, cloud cover, male plumage morph x date	6	573.46	0.96	0.0220
Location, wind force, cloud cover, date	9	573.87	1.37	0.0179
Location, wind force, cloud cover, male plumage morph x date	9	573.91	1.42	0.0175
Location, flock size	4	574.08	1.59	0.0161
Location, male plumage morph, wind force, cloud cover, date	10	574.27	1.78	0.0147
Location, male plumage morph, wind force, flock size	8	574.38	1.88	0.0139
Location, male plumage morph, wind force, date	8	574.38	1.88	0.0139
Location, feeding habitat	4	574.41	1.92	0.0137
Location, cloud cover, date	6	574.45	1.95	0.0134
Location, male plumage morph, wind force, male plumage morph x date	8	574.48	1.98	0.0132
Location, flock size, male plumage morph x date	5	574.48	1.99	0.0132
Location, male plumage morph, feeding habitat, wind force	8	574.49	1.99	0.0132
Location, wind force, date	7	574.49	2.00	0.0131
Location, male plumage morph, flock size	5	574.51	2.01	0.0130
Location, date	4	574.53	2.03	0.0129
Location, wind force, cloud cover	8	574.75	2.25	0.0115
Location, male plumage morph, feeding habitat	5	574.76	2.26	0.0115
Location, wind force, flock size, male plumage morph x date	8	574.76	2.27	0.0115
Location, male plumage morph, date	5	574.77	2.28	0.0114
Location, wind force, cloud cover, date, male plumage morph x date	10	574.78	2.29	0.0113
Location, cloud cover, flock size	6	574.80	2.30	0.0113
Location, date, male plumage morph x date	5	574.88	2.38	0.0108
Location, wind force, date, male plumage morph x date	8	574.88	2.38	0.0108
Location, feeding habitat, male plumage morph x date	5	574.90	2.40	0.0107
Location, cloud cover, flock size, male plumage morph x date	7	574.91	2.41	0.0107
Location, male plumage morph, male plumage morph x date	5	574.97	2.47	0.0104
Location, male plumage morph, cloud cover, flock size	7	574.97	2.47	0.0104
Location, feeding habitat, wind force, male plumage morph x date	8	574.99	2.49	0.0102
Location, male plumage morph, feeding habitat, cloud cover	7	575.10	2.61	0.0097
Location, feeding habitat, cloud cover	6	575.11	2.61	0.0097
Location, feeding habitat, cloud cover, male plumage morph x date	7	575.21	2.71	0.0092
Location, male plumage morph, wind force, cloud cover, flock size	10	575.27	2.77	0.0089
Location, male plumage morph, feeding habitat, wind force, cloud cover	10	575.28	2.78	0.0089
Location, male plumage morph, wind force, cloud cover, male plumage morph x date	10	575.32	2.82	0.0087

Table A7 (cont.)

Variables included	Df	AIC	ΔAIC	AIC weight
Location, male plumage morph, cloud cover, male plumage morph x date	7	575.32	2.82	0.0087
Location, male plumage morph, cloud cover, date	7	575.32	2.82	0.0087
Location, wind force, flock size	7	575.36	2.87	0.0085
Location, cloud cover, date, male plumage morph x date	7	575.37	2.88	0.0085
Location, feeding habitat, wind force	7	575.44	2.94	0.0082
Location, wind force, cloud cover, flock size, male plumage morph x date	10	575.76	3.26	0.0070
Location, feeding habitat, wind force, cloud cover, date	10	575.82	3.32	0.0068
Location, wind force, cloud cover, date, flock size	10	575.87	3.37	0.0066
Location, feeding habitat, wind force, cloud cover, male plumage morph x date	10	575.88	3.39	0.0065
Location, feeding habitat, flock size	5	575.98	3.48	0.0062
Location, date, flock size, male plumage morph x date	6	576.02	3.53	0.0061
Location, date, flock size	5	576.08	3.59	0.0059
Location, male plumage morph, date, flock size	6	576.12	3.63	0.0058
Location, feeding habitat, cloud cover, date	7	576.17	3.68	0.0057
Location, male plumage morph, feeding habitat, wind force, cloud cover, date	11	576.18	3.68	0.0057
Location, cloud cover, date, flock size	7	576.19	3.69	0.0056
Location, male plumage morph, wind force, cloud cover, date, flock size	11	576.26	3.76	0.0054
Location, male plumage morph, wind force, cloud cover, date, male plumage morph x date	11	576.27	3.77	0.0054
Location, male plumage morph, wind force, date, flock size	9	576.29	3.79	0.0054
Location, male plumage morph, feeding habitat, flock size	6	576.29	3.80	0.0053
Location, feeding habitat, flock size, male plumage morph x date	6	576.30	3.80	0.0053
Location, male plumage morph, wind force, flock size, male plumage morph x date	9	576.33	3.84	0.0052
Location, male plumage morph, feeding habitat, wind force, date	9	576.37	3.87	0.0051
Location, male plumage morph, feeding habitat, wind force, flock size	9	576.37	3.87	0.0051
Location, male plumage morph, wind force, date, male plumage morph x date	9	576.37	3.88	0.0051
Location, feeding habitat, date	5	576.38	3.88	0.0051
Location, male plumage morph, flock size, male plumage morph x date	6	576.40	3.91	0.0051
Location, wind force, date, flock size	8	576.46	3.97	0.0049
Location, male plumage morph, feeding habitat, wind force, male plumage morph x date	9	576.47	3.97	0.0049
Location, feeding habitat, wind force, date	8	576.49	3.99	0.0048

Table A8 Results of Wald statistics testing for effects of seven predictor variables (included in the GLMs; see Table A7) on peck rate of foraging Ruffs

Variable	**Df**	**Wald statistic**	***P***
Constant	1	441.41	<0.001
Location	3	32.77	<0.001
Male plumage morph	1	0.53	0.466
Feeding habitat	1	0.09	0.762
Wind force	3	6.75	0.080
Cloud cover	2	4.37	0.113
Date	1	0.99	0.319
Flock size	1	0.01	0.930
Male plumage morph x date	1	<0.01	0.960

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